# The Prairies of the E. Lucy Braun Preserve, Adams County, Ohio: A Soil Study[1]

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ABSTRACT. **Analysis of samples of the 0 to 10-cm soil depth collected at 65 locations under six vegetation communities showed that prairie and cedar-hardwood communities occurred on calcareous (range, pH 6.9-7.9) soils with low silt concentrations (20–54%), and that pine and oak communities occurred on acid (pH 4.3-6.3) soils with high silt (54-80%); this represented a distinction between communities on soils derived from dolomite and those on soils derived primarily from shale. Greater masses of plant opal were extracted from soils on dolomite (median, 2.4 kg/m$^2$) compared to shale (0.9 kg/m$^2$), suggesting that opal-depositing plant species had played a more important role in the vegetative history of the dolomite soils. Opal mass in dolomite soils did not, however, differ between soils presently under forests and those under prairies; all dolomite areas seemed to have had the same general vegetative history, one involving successive intervals of occupancy by both prairie and forest vegetation. Although opal was abundant on dolomite, shapes diagnostic of grasses were infrequently encountered in the soil, indicating that phytolith-rich forbs as well as grasses may have been important constituents of these forest openings in the past. The distinction between "primary" prairies (natural prairies) and "secondary" prairies (prairies formed by human disturbance of forests) was judged to be of limited applicability to the study area since prairies seemed to occur only on areas of soil derived from dolomite, and since prairie and forest vegetation were interpreted as having naturally alternated over time on these areas.**

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## INTRODUCTION

At the time of European settlement, tall-grass prairies occurred throughout southern Ohio and adjacent states in the form of a fragmented "peninsula" (Transeau 1935) or an "archipelago" (Sears 1981) of patches extending eastward into the deciduous forest region from the extensive grasslands of the mid-continent. Inherent to this patchy distribution was a great length of boundary separating prairies from forests. Such boundaries are unstable (Tomanek and Hulett 1970, Wells 1970, Sears 1981, Annala and Kapustka 1983, Annala et al. 1983, Kline and Howell 1987), shifting rapidly in response to even subtle variations in weather, fire regime, and human disturbance. Since settlement, this instability has manifested itself as forest expansion onto prairies and, perhaps less commonly, as prairie colonization of areas originally occupied by forest but cleared and subsequently abandoned (Shimek 1911, Cusick 1981). The latter type of boundary shift, prairies expanding onto forest land, was recognized by Braun (1928) when she defined "primary" prairies as those that existed prior to European settlement, and differentiated these from "secondary" prairies, or those that developed as a result of European disturbance.

The Edge of Appalachia Preserve System (E-of-A) in Adams County, OH, is a collection of over 50 prairie patches that is jointly managed by the Cincinnati Museum of Natural History and the Ohio Chapter of The Nature Conservancy. The plants forming the prairies, and the associated animals, are not common in the surrounding deciduous forests, hence E-of-A contains locally rare examples of the tall-grass prairie ecosystem. Some understanding of the former extent of these prairies, and the ability to distinguish between primary and secondary prairies, would aid in interpreting the present distribution of prairie patches and in choosing management techniques effective in preserving both the prairies and forest communities found on E-of-A.

Phytoliths, or plant opal, are small (mostly <50 x 10$^{-3}$ mm) grains that occur in plant tissues, primarily in the foliage. Phytoliths are formed through the passive uptake of Si from the soil solution, its movement in the transpiration stream, and precipitation as opal in cells and cell walls as water is lost from the foliage (Simkiss and Wilbur 1989). Upon decomposition of the enclosing tissues, phytoliths are released into the soil and may persist for long periods of time (e.g. 13,300 ± 450 yrs, Wilding 1967).

Plant species differ in the amount and shape of phytoliths formed in their foliage. Distinctive dumbbell-shaped opal is recognized as diagnostic of the Panicoid group of grasses (Drees et al. 1986, Piperno 1989), including the genera *Andropogon* and *Sorghastrum* which are important constituents of tall-grass prairies such as those of E-of-A. In addition, the foliage of most species of grass contains a much higher opal concentration than the foliage of most species of trees, and on an annual basis, grasslands commonly contribute five to ten times as much opal to the soil as do forests (Drees et al. 1986). Thus, if boundaries separating tall-grass prairies and forests were stable for long periods of time, prairie soils would contain relatively large masses of opal, and diagnostic dumbbell shapes would be present. Similarly, soils under primary prairies would contain greater masses of opal than soils under secondary prairies of recent origin.

The present study used opal analysis to examine the vegetative history of a part of E-of-A. Existing plant communities were the basis for stratifying the landscape and collecting soil samples. Phytolith mass and shape were then compared among communities. The objective was to examine the related questions of prairie-forest

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boundary stability, and of primary *versus* secondary prairie origin.

## STUDY AREA

This research was conducted on the E. Lucy Braun Preserve (Lynx Prairie Preserve), a ~22-ha part of E-of-A in eastern Adams County, about 1.2 km south of the town of Lynx (38°45'N, 83°22' W). The climate is continental with mean annual precipitation of 1,083 mm and mean annual temperature of 12° C (NOAA 1985).

The study area lies south of the limits of Pleistocene glaciation near the edge of the escarpment separating the Kanawha Section of the Appalachian Plateaus Province from the Lexington Plain Section of the Interior Low Plains Province to the west (Bier 1967). The topography is gently to steeply sloping, with elevations ranging from 227 to 344 m above mean sea level. Above elevations of ~258 m, the surficial bedrock on the study area is the Devonian Ohio Shale; at lower elevations, surficial rocks are Silurian dolomites, primarily the Peebles, with the Lilley and Bisher Dolomites limited to elevations below ~235 m (K. O'Bryan, pers. comm.).

Although thin layers of loess may be locally present, soils have formed chiefly in residuum and colluvium from shale and dolomite, and depth to bedrock ranges from <10 cm to >100 cm. Soil profiles on acid substrates derived primarily from shale are similar to soils mapped as Typic Hapludults; profiles on calcareous substrates derived primarily from dolomite are more variable and correspond roughly to soils mapped as Lithic and Typic Hapludalfs (Lucht and Brown 1988).

European settlement of the Adams County area began about 1800 (Braun 1928). Disturbance was variable and locally severe, including utilization of prairies for crops and pasture; clearance of forests; and harvest of trees for wood, charcoal, and tan-bark (Braun 1928, Annala et al. 1983). By 1950, most fields and pastures on the study area had been abandoned (Annala et al. 1983). Today, the imprint of 150 yrs of human use remains in the form of old roads, fence lines, house sites, and other cultural features. Less obvious but ecologically more important effects of past land-use include: soil erosion; the introduction of exotic plant species such as Japanese honeysuckle (*Lonicera japonica*) and periwinkle (*Vinca minor*); altered natural successional patterns resulting, for example, in a dramatic increase in the importance of Virginia pine (*Pinus virginiana*) over the last 50 yrs (compare Table 1 of the present study with p. 453–456 of Braun 1928); and changes in area and spatial distribution of prairies and forests (e.g. Fig. 3 of Annala et al. 1983).

## MATERIALS AND METHODS

### Field

Grid points were installed on a 20- by 20-m spacing over ~15 ha of the Preserve as a reference for mapping natural and cultural features. Six vegetation communities (prairie, cedar-hardwood, pine-cedar, pine, oak, and bottomland) were identified and mapped. The study area was thus divided into 65 individual "map units" corresponding to stands of uniform vegetation (Fig. 1); these individual map units served as the basis for all further sampling. Forest community composition was quantified for stems ≥10 cm diameter at 1.3 m above ground (DBH) using the point-quarter method (Brower and Zar 1984) at two random points in each of the 51 map units comprised of forest vegetation.

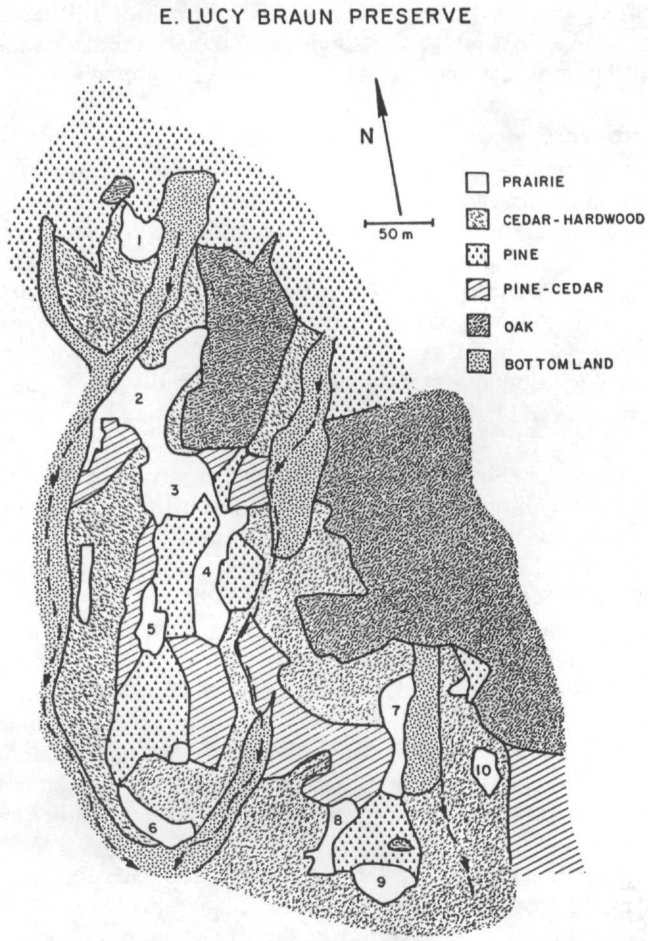


FIGURE 1. Distribution of six vegetation communities on the E. Lucy Braun Preserve, Adams County, OH. Dashed lines with arrows show the locations of major streams; numbers identify major prairie patches. Field work was done during the winter, 1988-89.

Samples of the 0 to 10-cm soil depth, in most cases composed entirely of A horizon material, were collected in each of the 65 map units. Samples were collected with a push tube (2-cm inside diameter) at five points in each map unit with five cores taken at each point; typically, these samples were collected within an area of ~250 m$^2$ except that sampling points were distributed over the entire area of each prairie. The 25 cores per map unit were composited to form a single sample for soil and opal analysis. Sampling was restricted to soil areas judged to be free of severe erosion; this observation was based on ground surface microtopography and soil color.

At a single point in each of two prairies, two cedar-hardwood map units, two pine units, and two oak units, samples were collected from a depth of 50 cm, or from just above bedrock in profiles shallower than 50 cm, to check for possible opal input from the parent material. At the same eight points, volumetric samples (120 cm$^3$) of the surface soil were collected to determine bulk density on the basis of field-volume and oven-dry mass. Soil profiles were examined at a number of points within each map unit to a depth of ~90 cm using a push tube and a field pH kit; this latter examination was useful in confirming spatial patterns of soils and parent materials indicated by surface soil properties.

### Laboratory

Samples were air-dried and sieved to remove fragments >2 mm. Subsamples (0.5 to 1.0 g) of all 65 samples were treated with an excess of 10% HCl to dissolve carbonates, and were dispersed in 5% Na-hexametaphosphate. The 0.01- to 0.05-mm fraction (referred to as "coarse silt" in this paper) was obtained by first removing particles >0.05 mm by wet sieving, and then removing particles <0.01 mm by five to nine repetitions of sedimentation (of the >0.01 mm fraction) and decantation (of the <0.01 mm fraction) based on Stokes Law calculations for particles with specific gravity (s.g.) of 1.9. Phytoliths were extracted from the coarse silt using techniques similar to those described by Piperno (1988). A heavy liquid (s.g. 2.3) was prepared from bromoform and ethanol, and phytoliths were removed from the coarse silt by four to six sink-float extractions. Phytolith concentration in the coarse silt was corrected for contamination by counting crystalline grains under a polarizing microscope and assuming all of these were quartz (s.g. 2.65). Total phytolith mass in the 0 to 10-cm depth was calculated on a whole-soil basis (kg/m$^2$) using the corrected opal concentration (kg per kg coarse silt), percentage coarse silt (kg per kg soil), soil bulk density (kg per m$^3$ soil), and sampling depth (m).

One thousand phytoliths from soils of each vegetation community were examined in 400X to quantify the percentage occurrence of diagnostic dumbbell shapes. Shapes extracted from soil were also compared to a reference collection of phytoliths extracted from foliage in a related study (Kalisz and Boettcher 1990) to gain information concerning the taxonomic origin of opal in soil.

Total nitrogen was determined for all samples using a Kjeldahl procedure (Bremner and Mulvaney 1982), and extractable Ca using the Mehlich 3 extractant (Mehlich 1984). Soil pH was measured in 1:1 mixtures (w/v) of soil:water. Particle-size distribution was determined for a subset of 28 samples by the hydrometer method (Gee and Bauder 1986) after removing organic matter with NaOCl.

### Data Analysis

Opal and soil properties were statistically compared among the prairie, cedar-hardwood, pine, and oak communities, which together occupied >80% of the study area, using nonparametric Kruskal-Wallis tests evaluated at the 0.01 level of significance. Where significant differences were found, equations presented by Conover (1980) were used to separate vegetation communities into statistically distinct groups.

Medians and ranges are presented in the text and tables together with the results of the nonparametric comparisons of the distributions. All references to specific prairies are keyed to the numbers on Figures 1 and 2. Plant nomenclature is according to Gleason and Cronquist (1963).

## RESULTS

### Vegetation

Prairies were dominated by grasses and forbs, most obviously by little bluestem (*Andropogon scoparius*), Indian grass (*Sorghastrum nutans*), and big bluestem (*A. gerardi*). Coverage and species occurrence were variable within and among prairies (e.g. *Echinacea purpurea* occurred only on Prairie 10) with substantial areas of bare soil and of dominance by forbs (e.g. by *Silphium terebinthinaceum* on Prairie 3). Braun (1928) recorded 199 herbaceous species from the prairies of Adams County including 43 species of Compositae, 27 of Gramineae, and 17 of Fabaceae.

Forest communities differed in species importance (Table 1) and in stand structure. The bottomland (20.6 m$^2$/ha basal area; 513 stems/ha density), cedar-hardwood (18.1 m$^2$/ha; 637 stems/ha), and oak (36.7 m$^2$/ha; 564 stems/ha) communities were similar to communities described by Braun (1928), whereas the pine (37.8 m$^2$/ha; 747 stems/ha) and pine-cedar (26.2 m$^2$/ha; 855 stems/ha) communities represent recent expansion of Virginia pine onto formerly open or cleared land. The cedar-hardwood community was most variable, ranging from mixed mesophytic forests on protected slopes to open chinkapin oak (*Quercus muehlenbergii*) and redcedar (*Juniperus virginiana*) stands on upper slopes and rocky areas. The cedar-hardwood community occupied approximately 33% of the study area; pine, 22%; oak, 14%; pine-cedar, 12%; prairie, 11%; and bottomland, 8% (Fig. 1).

Prairies occurred on the full range of available landscape positions including southeastern upper side slopes (Prairies 4 and 7); southeastern lower side slopes (Prairie 1); southwestern nose slopes (Prairies 6 and 9); northwestern side slopes (Prairie 2); and ridgetops (Prairies 3, 5, 8, and 10) (Fig. 1). As Braun (1928) reported for Adams County in general, all prairies in the study area were located on dolomite; Prairie 6 was at an elevation corresponding to the Lilley Dolomite, and all others were at elevations corresponding to the Peebles Dolomite (K. O'Bryan, pers. comm.). In many locations, boundaries between prairies and the cedar-hardwood community were diffuse (e.g. western boundary of Prairie 3) with redcedar, buckthorn (*Rhamnus caroliniana*), redbud (*Cercis canadensis*), and persimmon (*Diospyros virginiana*) invading the prairies. Although some small Virginia pines were found on prairies, boundaries between prairies and pine and between prairies and oak were generally abrupt; successful invasion of prairies by dominants of either of these communities was not observed.

### Soils

Soil pH and concentrations of N, Ca, and coarse silt differed substantially between prairies and cedar-hardwoods *versus* pine and oak (Table 2). Soil properties under the pine-cedar community were generally intermediate; medians for the latter were 42% coarse silt and pH 6.8. Differences in pH, Ca, and N between prairie and cedar-hardwood soils were statistically significant (Table 2), but the magnitudes of the differences were small and were likely of little biological significance.

Coarse silt concentrations, taken together with pH, suggested that a single soil parent material occurred in the upper 10-cm depth under prairies and cedar-hardwood, and that this parent material differed from that under the pine and oak communities (Table 2). Particle-size distributions

TABLE 1

*Importance of tree species (stems ≥ 10 cm DBH) in five forest communities (sample sizes in parentheses) on the E. Lucy Braun Preserve. 1989.*

| Species | Importance† (%) Cedar-Hardwood (36) | Pine-Cedar (18) | Pines (20) | Oak (20) | Bottomland (8) |
|---|---|---|---|---|---|
| *Juniperus virginiana* | 40 | 36 | 6 | 9 | 6 |
| *Quercus muehlenbergii* | 26 | 0 | 0 | 0 | 2 |
| *Liriodendron tulipifera* | 12 | 4 | 3 | 1 | 7 |
| *Cercis canadensis* | 4 | 1 | 0 | 0 | 2 |
| *Acer saccharum* | 4 | 0 | 0 | 1 | 0 |
| *Ostrya americana* | 3 | 0 | 0 | 1 | 0 |
| *Fraxinus americana* | 3 | 1 | 0 | 2 | 8 |
| *Pinus virginiana* | 2 | 57 | 83 | 5 | 0 |
| *Cornus florida* | 2 | 0 | 3 | 5 | 0 |
| *Quercus imbricaria* | 1 | 1 | 0 | 0 | 0 |
| *Quercus palustris* | 1 | 0 | 0 | 0 | 0 |
| *Ulmus americana* | 1 | 0 | 0 | 0 | 19 |
| *Carya* spp. | 1 | 0 | 1 | 13 | 0 |
| *Populus grandidentata* | 0 | 0 | 2 | 5 | 0 |
| *Acer rubrum* | 0 | 0 | 1 | 0 | 0 |
| *Oxydendrum arboreum* | 0 | 0 | 1 | 0 | 0 |
| *Quercus alba* | 0 | 0 | 0 | 45 | 9 |
| *Quercus velutina* | 0 | 0 | 0 | 5 | 8 |
| *Quercus rubra* | 0 | 0 | 0 | 3 | 0 |
| *Quercus stellata* | 0 | 0 | 0 | 3 | 0 |
| *Nyssa sylvatica* | 0 | 0 | 0 | 1 | 0 |
| *Fagus grandifolia* | 0 | 0 | 0 | 1 | 0 |
| *Plantanus occidentalis* | 0 | 0 | 0 | 0 | 36 |
| *Prunus serotina* | 0 | 0 | 0 | 0 | 3 |

† Importance = [(relative basal area + relative density)/2] 100

TABLE 2

*Medians (ranges) of selected properties of the 0 to 10 cm soil depths under four plant communities on the E. Lucy Braun Preserve.*

| Community (n) | pH | Ca cmol(+)/kg | Total N mg/kg | Coarse† Silt % | Opal kg/m² |
|---|---|---|---|---|---|
| Prairie (10) | 7.7[a*] (7.4-7.9) | 14.8[e] (10.9-20.3) | 2900[h] (1900-4500) | 20[k] (7-39) | 2.6[l] (1.4-4.9) |
| Cedar-Hardwood (16) | 7.5[b] (6.9-7.7) | 17.9[d] (14.2-21.3) | 3700[g] (2100-5000) | 32[k] (9-51) | 2.2[l] (0.8-3.7) |
| Pine (9) | 5.1[c] (4.4-6.3) | 5.6[f] (1.5-10.7) | 1500[i] (1100-2800) | 52[j] (45-64) | 0.9[m] (0.5-1.2) |
| Oak (10) | 4.6[c] (4.3-5.6) | 1.6[f] (0.6-6.3) | 1300[i] (1100-1900) | 55[j] (47-70) | 0.9[m] (0.2-1.3) |

† Coarse silt is the $10x10^{-3}$ to $50x10^{-3}$ mm fraction.
*Distributions of individual properties differ nonparametrically at the 0.01 level among communities designated with different letters.

supported this conclusion; prairies and the cedar-hardwood community occurred on a parent material with relatively low silt, whereas the pine and oak communities occurred on a parent material with relatively high silt (Table 3). Examination of soils to a depth of 90 cm at numerous locations on the study area confirmed the relationship between vegetation community and soil parent material on upland locations. In all cases, sola under the prairie and cedar-hardwood communities had low silt concentrations and high pHs, and in most cases, sola under the oak and pine communities had high silt and low pHs. The exceptions to this pattern were the pine "islands" in the vicinities of Prairies 3, 5, and 9 (Fig. 1) where acid, high-silt surface soils changed abruptly to basic, low-silt soils at depths ranging from 10 to 50 cm. These exceptions likely represented isolated bodies of shallow shale residuum, or of shallow mixtures of loess and shale residuum, overlying dolomite residuum (Fig. 2).

### Opal

Opal mass in the 0 to 10-cm soil depth differed significantly between prairies and cedar-hardwood *versus* oak and pine (Table 2). Opal mass in shale soils was low and relatively uniform, ranging from 0.2 to 1.3 kg/m² (Table 2), with 90% of the masses between 0.5 and 1.0 kg/m². In contrast, opal mass ranged from 0.8 to 4.9 kg/m² on dolomite (Table 2). Four prairies (Prairies 4, 6, 7, and 9) and two cedar-hardwood areas (areas to either side of Prairie 6) comprised the six sample locations on dolomite with the highest opal contents (i.e. the upper 25% of all locations on dolomite); these locations were all on slopes with southerly orientations and gradients >15%, and the four prairies had generally shallow soils and extensive areas of rock outcrops. Conversely, of the six sample locations on dolomite with the lowest opal contents, four were on protected slopes under mixed mesophytic forest; one was on a flat ridgetop under oak and redcedar; and one was a prairie (Prairie 3) on a flat ridgetop with generally deep soils.

Analysis of opal shape, although successfully used to interpret grassland-forest boundary stability in other areas (e.g. Kalisz and Stone 1984, Bartolome et al. 1986), was not useful in separating prairie and forest soils on the E. L. Braun Preserve. Few dumbbells were observed, and these were found under both prairie and forest, and in both dolomite- and shale-derived soils. As noted also on another prairie patch in southeastern Ohio (Kalisz and Boettcher 1990), opal shapes extracted from soils were indistinguishable from shapes extracted from the foliage of various herbaceous dicots found on prairies.

TABLE 3

*Median (range) percentages of sand ($50x10^{-3}$ to 2 mm), silt ($2x10^{-3}$ to $50x10^{-3}$ mm), and clay ( < $2x10^{-3}$ mm) in the 0 to 10 cm soil depths under two vegetation-substrate combinations on the E. Lucy Braun Preserve.*

| Vegetation and Substrate (n) | Sand* | Silt* | Clay* |
|---|---|---|---|
| Prairie and Cedar-Hardwood on Dolomite (18) | 33 (12-54) | 40 (20-54) | 26 (13-39) |
| Pine and Oak on Shale (10) | 15 (7-23) | 69 (54-80) | 14 (4-30) |

* Distributions of all particle sizes differ nonparametrically at the 0.01 level between vegetation-substrates.

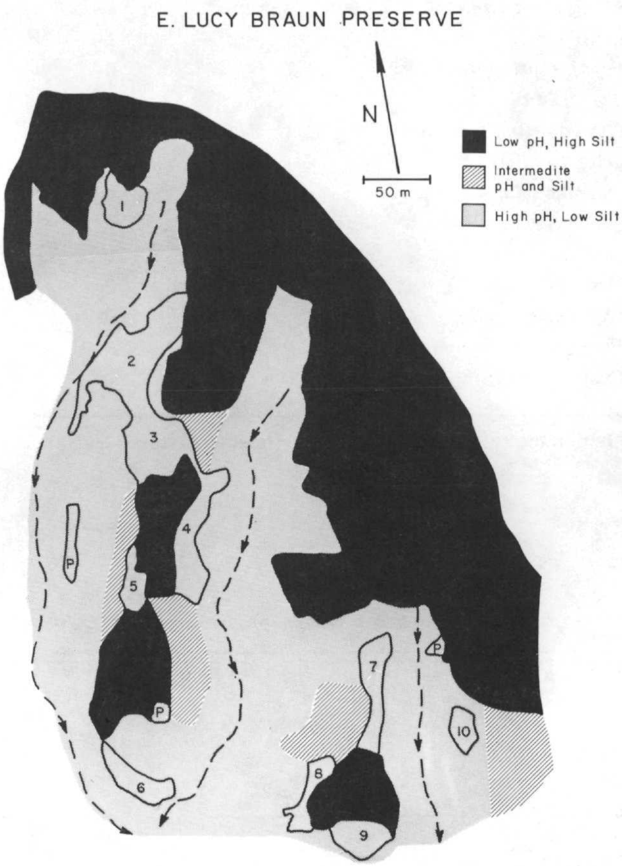


FIGURE 2. Distribution of three types of surface soils on the E. Lucy Braun Preserve, Adams County, OH. Dashed lines with arrows show the locations of major streams; numbers identify major prairie patches.

## DISCUSSION

Prairies and cedar-hardwood occurred on calcareous, low-silt material, presumably dolomite residuum; pine and oak occurred on acid, high-silt material, presumably shale colluvium that was >50 cm thick on the northeastern periphery of the study area and 10 to 50 cm thick under the pine "islands" in the vicinities of Prairies 3, 5, and 9. Pine-cedar occurred on a material with intermediate characteristics, presumably a layer of shale-derived soil <10 cm thick, or a mixture of materials from dolomite and shale (Figs. 1, 2). Characteristics of both surface soils (Tables 2, 3) and deep profiles support this interpretation. In addition, except for pine "islands" (Fig. 2) which occurred as outliers on the dolomite side of the shale-dolomite bedrock boundary, all units of prairie and cedar-hardwood vegetation occurred on areas underlain by dolomite, and all units of oak and pine occurred on areas underlain by shale. This judgement was based on elevational relationships between vegetation communities, locations of dolomite outcrops, and mapped surficial geology (K. O'Bryan, pers. comm.). In addition, not only silt concentrations, but also sand and clay concentrations differed significantly among communities (Table 3), and individual communities were not restricted to single landscape positions (Fig. 1). Taken together, this evidence supports our conclusion that soil differences among communities reflect different parent materials rather than variability caused by deposition or erosion of loess or colluvium.

It is well known (e.g. Boettcher and Kalisz 1990) that plant species differ in nutrient-cycling characteristics and that this may lead to differential accumulations of basic cations, N, and other substances in the uppermost soil layer, and to the development of distinctly different soil profiles under stands or individuals of contrasting species growing on a uniform parent material. The relatively subtle chemical differences between prairie and cedar-hardwood soils on dolomite residuum (Table 2) provide an example of such an effect; differences of the same magnitude as reported here between prairie and cedar-hardwood were found by White and Reicken (1955) when comparing forest and prairie soils developed on a single parent material. The extreme contrasts in the chemical properties of the surface layers of prairie and cedar-hardwood soils on the one hand, and oak and pine soils on the other (Table 2) cannot, however, be ascribed to differences in nutrient-cycling: past research has clearly shown that the magnitude of plant-induced soil variability is much less than found here even when comparing very old individuals of species with strikingly different nutrient-cycling characteristics (Zinke and Crocker 1962, Alban 1969, Boettcher and Kalisz 1990).

The simplest interpretation of our results is that the prairie and cedar-hardwood communities were restricted to calcareous surface soils derived from dolomite, whereas the pine and oak communities were restricted to acid surface soils derived from shale. This indicates that vegetation communities on the E. Lucy Braun Preserve clearly reflect the lithologic origin of at least the surface soil or A horizon, and is in accord with Braun's (1928) conclusion that community composition of all successional stages in Adams County is most strongly controlled by the type of bedrock. This result also suggests that past changes in the boundaries of prairies most likely occurred only on dolomite as prairies expanded, contracted, or shifted over the landscape; interchange of prairie and forest species across the dolomite-shale bedrock contact was less likely, hence prairie-forest boundaries that coincided with bedrock boundaries were stable.

The low frequency of dumbbell-shaped phytoliths, even on areas presently occupied by tall-grass species, may be accounted for simply by their dilution in the soil by large numbers of phytoliths derived from other plant taxa. Most species of trees, including the genera *Quercus, Pinus,* and *Carya* (Geis 1973, Klein and Geis 1978), and the species *Juniperus virginiana* and *Pinus virginiana* (Boettcher and Kalisz, unpublished), have foliage opal concentrations <<1%. Conversely, many species of prairie forbs have opal concentrations >>2% (Kalisz and Boettcher 1990), that is of the same order of magnitude as grasses. Thus, in addition to grasses, forbs may have been important constituents of forest openings in Adams County at various times in the past, and may have provided the abundant opal that now masks the diagnostic forms derived from tall-grass species.

Greater masses of opal in soils under communities on dolomite *versus* those on shale (Table 2) suggests that opal-depositing grass and forb species have played a more important role in the vegetative history on dolomite. These greater masses cannot be ascribed to either increased availability or increased inheritance of Si from dolomite since: 1) Uptake of Si is proportional to concentration in solution (Sangster 1970), and this concentration decreases as pH increases, especially above pH 10 (Drees et al. 1986). In the absence of differing vegetative histories, lesser amounts of phytoliths would thus be expected on calcareous dolomite soils compared to acid shale soils. 2) Opal concentrations below the A horizon were uniformly low under all types of vegetation (median at 50 cm, 0.3% *vs.* a range of 1.1 to 2.2% in the surface), eliminating the possibility of inheritance of large opal quantities from the dolomite bedrock. Opal extracted from soils must therefore be of plant origin, and input has been greater on dolomite than on shale soils.

In the typical case on dolomite, opal mass did not differ between soils presently under prairie and those under the cedar-hardwood community (Table 2). This means that the long-term vegetative history has been generally uniform over all areas on dolomite regardless of present occupancy by prairie or forest. Within these areas of generally uniform vegetative history, however, variability in opal mass in soils may be interpreted as caused by more frequent or longer occupancy of the least favorable landscape positions by prairies rather than by forests. Prairies may have been most important in the vegetative history on southerly slopes and areas of shallow soil, and least important on protected slopes and areas of deep soil. Present contacts between forests and prairies on dolomite are unstable, and prairie patches have undoubtedly varied in size and location since prairie species first arrived in the region. Based on opal and soil analyses, similar conclusions were reached regarding prairie-forest boundary stability in western Ohio (Wilding and Drees 1968, 1971) and in east-central Illinois (Jones and Beavers 1964), where post-glacial vegetative history on areas presently occupied by prairie was summarized as including only "short intervals" of prairie during a "complex history of plant transgressions" (Wilding and Drees 1968), and as "constantly oscillating vegetation zones...with a preponderance of woody types" (Jones and Beavers 1964). Likewise, the vegetative history of the study area probably involved shifting areas of prairie and forest, with the added complexity that vegetation communities also differed between the two types of bedrock. Based on this interpretation, the distinction between primary and secondary prairies has little meaning since prairies only occur on areas of dolomite, and prairies and forests have alternated over time on these areas.

From a management perspective, the results of the present study imply that only members of the cedar-hardwood community can effectively encroach on prairies; Virginia pine, white oak, and other species typical of the pine and oak communities do not seem to successfully, or at least rapidly, invade the dolomite substrate. Thus, prairie-forest boundaries on dolomite may be artificially stabilized by cutting, girdling, or burning trees in or on the edge of the prairies. Given the natural interchange of dominance by prairies and the cedar-hardwood community, prairies could be encouraged to expand by clearance of forests on dolomite. This would mimic past vegetation shifts, and in this sense would not be unnatural. Since prairies established by forest clearance on dolomite are often indistinguishable from primary prairies (Braun 1928), intentional creation or enlargement of prairie patches, especially on droughty landscape positions, should prove to be a dependable and ecologically-sound way of ensuring the preservation of maximum species diversity on the Edge of Appalachia Preserve System.

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